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Gastrovascular Circulation in an Octocoral: Evidence of Significant Transport of Coral and Symbiont Cells

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Abstract. The gastrovascular system in the Red Sea soft coral *Parerythropodium fulvum fulvum* comprises two interconnected networks of canals filled with fluid and circulating cells. The first network is composed of narrow canals (50–80 μm in width) located below the upper ectodermal layer; the second network includes larger canals (300–500 μm in width) that are located deeper in the coral tissue. Particle movement in the second network is faster than in the superficial network, but in both, coral cells with and without healthy zooxanthellae circulate freely. To investigate the movement of metabolites and cellular components within the colony, coral fragments were exposed to ^{14}C-labeled seawater for 24 h in the laboratory and *in situ* under saturating photosynthetic photon flux and then grafted back to their original colonies. Grafts fused after 24 h. In the laboratory experiment, up to 45% of the fixed ^{14}C was translocated to the unlabeled colony within 48 h after fusion. In the *in situ* experiment, significant translocation of labeled materials occurred at the furthest parts of the colonies, 390 mm away from the fusion line, in 24 h. Even though the amount of labeling varied between colonies, labeled material spread throughout all the unlabeled parts. It thus appears that the gastrovascular system in *Parerythropodium fulvum fulvum* functions as an effective circulatory apparatus for fast translocation of organic compounds and cellular components within the colony.

Introduction

Corals are mostly colonial cnidarians composed of modular units (polyps) that, in a single colony, are physically connected and generally share similar physiological and biochemical environments. Translocation of organic compounds between polyps could result from diffusion down a concentration gradient (Pratt, 1905; Murdoch, 1978a; Fang *et al.*, 1989) or from active transport in the fluid of the gastrovascular system (Gladfelter, 1983; Schlichter, 1991, 1992).

Gastrovascular systems have been studied in several cnidarian groups including hydromedusae (Roosen-Runge, 1967), hydroids (Rees *et al.*, 1970; Blackstone, 1996), gorgonians (Murdoch, 1978a, b), pennatulids (Musgrave, 1909; Parker, 1920; Brafield, 1969), hexacorallians (Gladfelter, 1983; Schlichter, 1991, 1992), and soft corals (Pratt, 1905). These systems have been suggested to function as (1) a hydrostatic skeleton allowing the colony to expand or retract (Chapman, 1974; Fautin and Mariscal, 1991), (2) a transport system for the distribution of substances between polyps in which extracellular digestion of organic material also takes place (Gladfelter, 1983; Schlichter, 1991, 1992), (3) a transport system for exchange of gases such as oxygen and carbon dioxide (Brafield and Chapman, 1967; Chapman, 1972), (4) an excretion system for waste metabolites (Schlichter, 1991), and (5) a system that controls the morphological development of colonies (Dudgeon and Buss, 1996). Gastrovascular systems have been described as ramified canal networks with blind ends and with back-and-forth movement of the internal fluid (Blackstone, 1996) propelled by either flagella (Gladfelter, 1983) or other mechanisms (Schierwater *et al.*, 1992). In some corals, the gastrovascular cavity is a flow-through system with many pores that are located near the crests of the sclerosepta of the external body wall and allow uni-directional movement of fluids (Schlichter, 1991, 1992). Anthozoan and hydrozoan gastrovascular systems are distinguished one from the other

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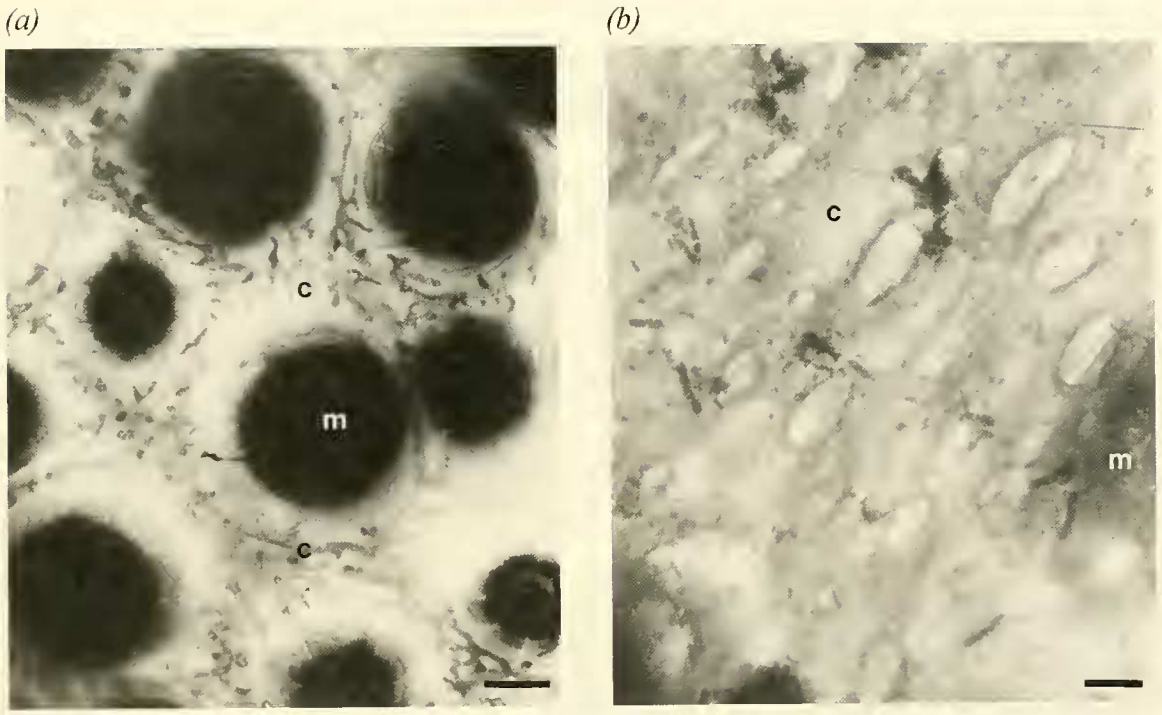


Figure 1. General morphology of the gastrovascular system of *Parerythropodium fulvum fulvum*. Superficial (a) and deep (b) network of canals in live specimens growing on glass slides. In photograph (b) the coral was positioned upside down with a strong back light to make the canals visible. m = mouth of a polyp, c = canal. Scale bars = 500 μm.

primarily by the presence of flagellated endodermal cells lining the entire internal gastrovascular epithelium of the anthozoans. This study refers mainly to the anthozoans.

Parerythropodium fulvum fulvum (Forskål, 1775), a symbiotic alcyonarian soft coral characterized by an encrusting growth form, a thin coenenchyme, and short polyp cavities, is common in shallow waters of the Israeli Red Sea coast (Benayahu and Loya, 1983). To further reveal the role of the gastrovascular system in this species, we investigated the structure and some physiological functions of this system. Here we document the free circulation of living animal cells and zooxanthellae within the gastrovascular system and the rapid transport of organic substances between different parts of the colony. These results suggest that the gastrovascular system in *P. f. fulvum* is a functional circulatory apparatus.

Materials and Methods

Collection and maintenance of corals

Colonies of *Parerythropodium fulvum fulvum* were collected at depths between 3 and 12 m in the Red Sea, next to the H. Steinitz Marine Biology Laboratory, Eilat, Israel. This encrusting coral is about 6-mm thick when growing on a straight surface; polyps emerge 3 to 10 mm from the base when expanded and have an average density of 22.6 polyps cm^{-2} (SD = 6.2; n = 8 different colonies). Colonies were carefully peeled off the substrate, reattached to glass slides by cotton threads, and transported to the National Institute of Oceanography at Haifa, Israel.

The corals were grown in the laboratory in 17-l aerated aquaria filled with running, 20-μm-filtered seawater at 24° ± 1°C. Photosynthetic photon flux (PPF) was provided by 500 W halogen lamps on a 12:12 h (light:dark) regime. On the surface of the aquaria the PPF, measured with a quantum meter (LI-COR, North Carolina), averaged 150 μmol photon m^{-2} s^{-1}, which is approximately the irradiance at a depth of 10 m in the Red Sea. Corals were fed twice a day with either 50-μm microcapsules of artificial plankton (Argent, Redmond, Washington), *Artemia nauplii* (Neptune Industries, Salt Lake City, Utah), or lyophilized rotifers.

Morphology

Specimens growing on the glass slides were observed with a binocular dissecting microscope at magnifications from 10× to 63×. For light microscopy, samples were fixed in 2.5% glutaraldehyde for 24 h, decalcified with formic acid and sodium citrate for 30 min (Rinkevich and Loya, 1979), dehydrated with ethanol, and embedded in glycol methacrylate plastic. Histological sections (width 2–3 μm) were stained with hematoxylin and eosin (Ban-

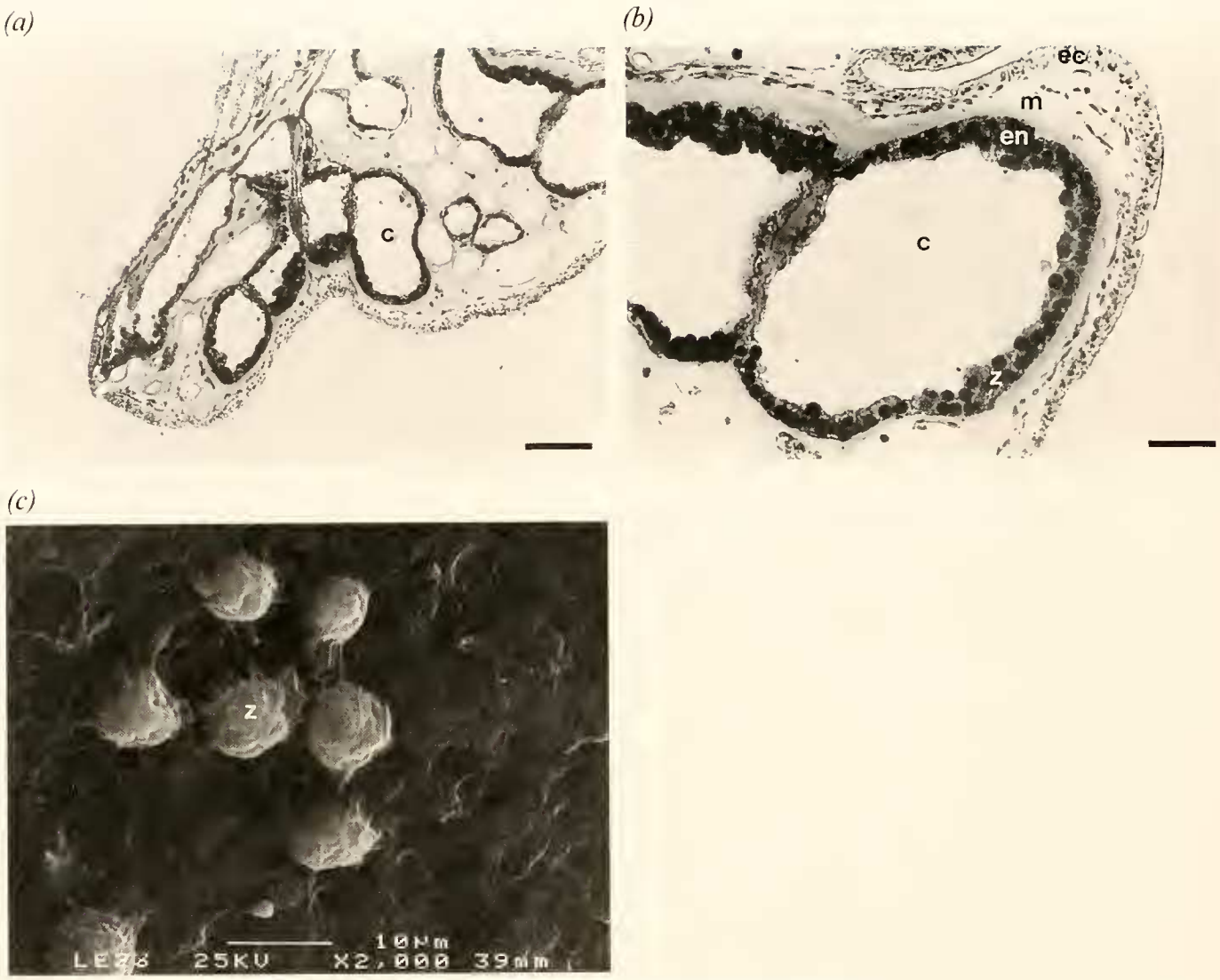


Figure 2. Detailed morphology of the gastrovascular system of *Parerythropodium fulvum fulvum*. (a, b) Cross-sections of the deeper canals inside the coral tissue. (c) Scanning electron micrograph showing algal cells embedded in endoderm within the inner wall of the canals. c = canal, ec = ectoderm, en = endoderm, m = mesoglea, z = zooxanthellae. Scale bars: a = 500 μm; b = 30 μm; c = 10 μm.

croft and Stevens, 1990). For scanning electron microscopy, specimens were fixed in 2.5% glutaraldehyde (electron microscopy grade) in filtered seawater, and sections were prepared following Bancroft and Stevens (1990).

Circulation of free cells

The presence of free circulating cells in the gastrovascular system was determined in three ways: (1) by collecting gastrovascular fluid from the mouth of the polyps and from inside the canals (fluid was obtained using a micromanipulator [Narishige, Japan], a microinjector [Narishige, IM 300, Japan] and a micropipette with a tip diameter of 30 μm) and viewing it with a light microscope (100×–1000×); (2) by analyzing histological cross-sections of the gastrovascular canals; and (3) by using a sharp razor blade to injure live corals in the periphery of the colony and observing the outcoming fluid under the light microscope.

To measure the movement of free cells in the canals, corals growing on glass slides were observed under the binocular dissecting microscope with strong background light. The movement rate of particles inside the gastrovascular system was timed by using a built-in grid located in the ocular of the dissecting microscope.

^{14}C labeling

Coral fragments from six colonies growing in the laboratory and six large colonies growing in the field were

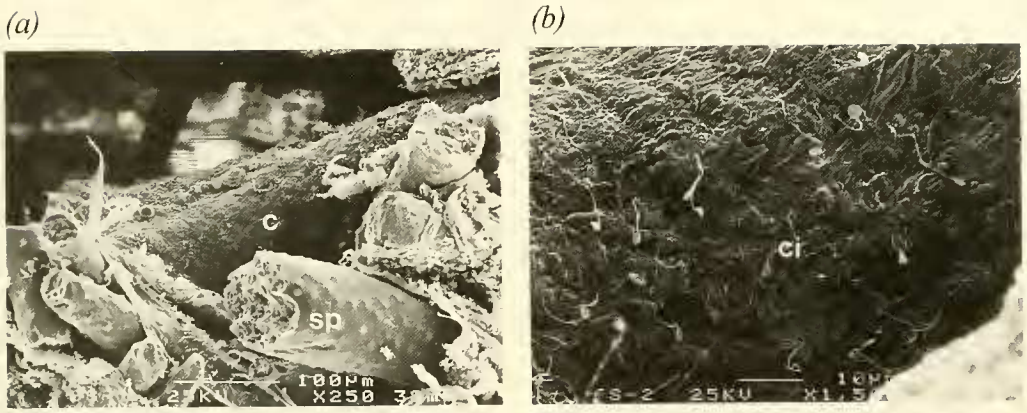


Figure 3. Scanning electron micrograph of the inner walls of a canal from the gastrovascular system of *Parerythropodium fulvum fulvum*. (a) This sample was frozen and then fractured to show the inner part of a canal. (b) Closer view of the inner wall covered with cilia. c = canal, ci = cilia, sp = spicula. Scale bars: a = 100 μm; b = 10 μm.

cut 24 to 48 h before starting the experiments. The fragments were incubated for 24 h in closed, transparent 1-l plastic chambers filled with filtered (2 μm) seawater containing $NaH^{14}CO_3$ (Amersham, Netherlands; 0.01 μCi ml^{-1}) at 25°C under continuous illumination (300 μmol photon m^{-2} s^{-1}) and gentle stirring. Incubation was followed by two to three rinses with ^{14}C-free seawater and placement in the dark to eliminate unfixed ^{14}C. The seawater was changed daily until no traces of radioactivity were found in the medium, usually 2 days, and then the labeled fragments were grafted in the laboratory or *in situ* to their original colonies.

Within the next 24 h, the fragments usually reattached to the substrate and fused, which included the connection of the canals, with tissue of the original colonies (see Frank *et al.*, 1996). Tissue from the labeled fragments and the unlabeled colonies was sampled with a 5-mm-diameter metal cork-borer (0.196 cm^2) 12, 24, and 48 h after fusion for the laboratory experiments and 24 h after fusion for the field experiments. The distance of each sample from the fusion line was recorded. The samples were solubilized in 1 ml Soluene-350 (Packard, England) at 37°C for 24 h. To eliminate any remaining unfixed ^{14}C, 0.5 ml of a 1 *N* solution of HCl was added, followed by gentle aeration for 4 h. Radioactivity was measured with a liquid scintillation spectrophotometer (Kontron) using 4 ml of scintillation fluid (Optifluor, Packard, England). To evaluate possible passage of ^{14}C to the unlabeled fragment through the water, similar control colonies were placed close (2–3 mm) to but not in contact with the labeled grafts and later sampled as above.

Results

Morphology of the canal system

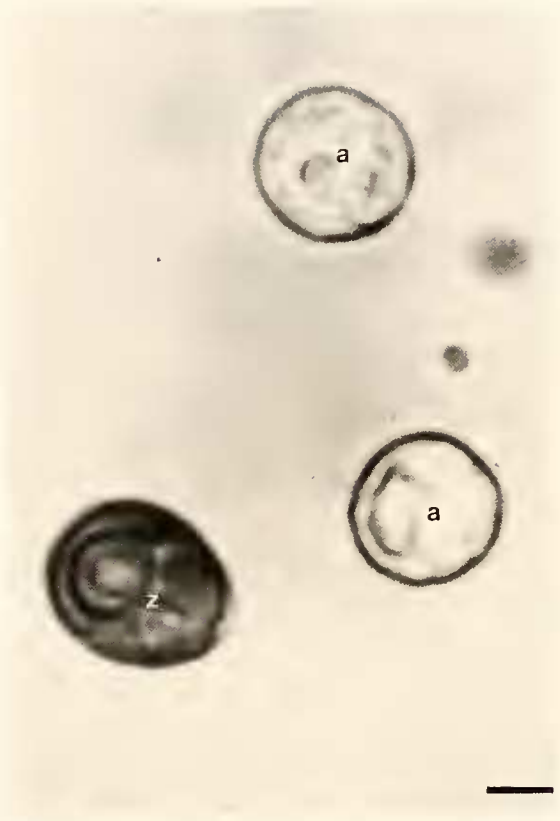
Observations of live colonies on glass slides revealed that the gastrovascular system in *Parerythropodium fulvum fulvum* comprises two distinctive, interconnected types of canals (Fig. 1) filled with moving fluid. The first type is superficial, lying just below the outer ectoderm layer and surrounding the polyps (Fig. 1a). The canals in this area were 50–80 μm in width, with abundant dead ends; the average speed of the particles in the fluid was 1.2 cm h^{-1} (n = 8; SD = 0.9) to either direction. The second type is deeper in the coenosarc and close to the base of the colony (Fig. 1b). These canals were 300–500 μm in width and the speed of their particles was much faster, averaging 3.4 cm min^{-1} (n = 10; SD = 1.1). In the superficial canals, zooxanthellae and coral cells were seen forming patches, but in deeper canals they moved freely with no apparent directionality.

Measurements on histological cross-sections (Fig. 2a, b), indicated that the gastrovascular cavity accounts for an average of 45% (n = 5; SD = 12.2) of the animal's volume. The inner wall of the canals is lined with endodermal cells possessing abundant zooxanthellae (Fig. 2b, c), with cilia covering most of the canal inner surface (Fig. 3a, b).

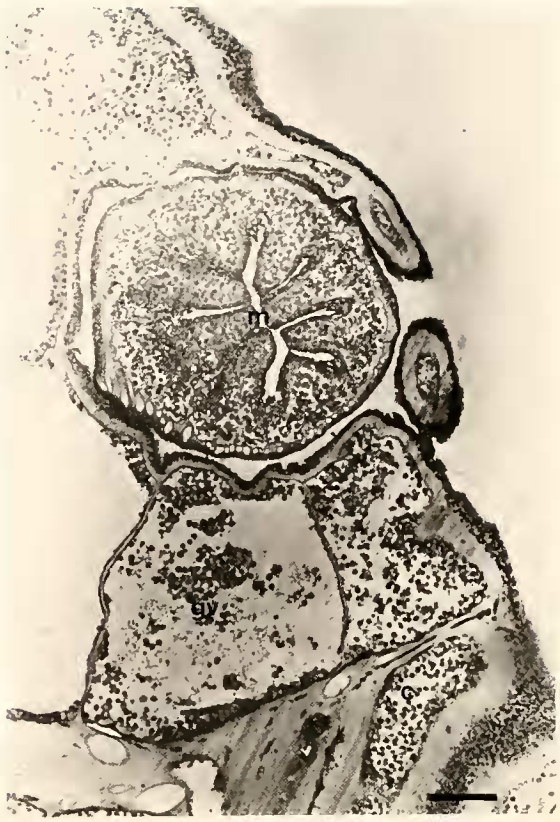
Circulation of free cells

Histological cross-sections from the gastrovascular cavity confirmed the presence of large quantities of free cells (Fig. 4a) inside the canals (Fig. 4b, c). Two types of cells circulated freely in the gastrovascular fluid collected from either polyp mouths or canals. Most (81.6%; SD = 5.4, n = 20 different coral colonies; 50 to 100 cells counted in each sample) were coral cells containing zooxanthellae, and the rest were coral cells without zooxanthellae. In addition, amorphous particles that may correspond to partly digested food were commonly seen in the gastrovascular fluid. When corals were slightly injured at the edge of the colony, large amounts of zooxanthellae

(a)



(b)



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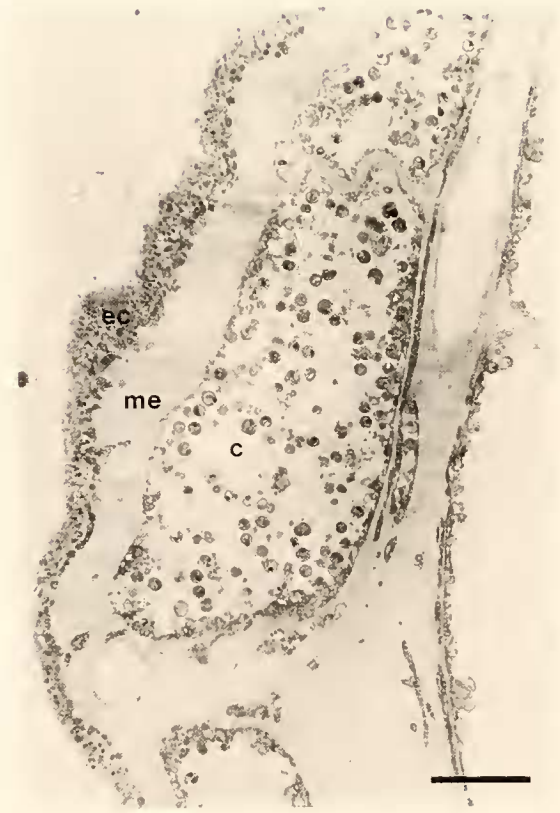

(d)

Table I

Translocation of ^{14}C over time in the laboratory experiment following fusions between the labeled fragments and their respective unlabeled coral colonies; (n) is the number of corer samples analyzed

Colony no.	Fragment size (cm^2)		Total ^{14}C (DPM)*		Time (h)	^{14}C transported (%)
	Labeled (n)	Unlabeled (n)	Labeled	Unlabeled		
1	3.28 (4)	18.28 (26)	157,442	2,756	12	1.7
2	4.97 (7)	52.56 (63)	288,025	12,092	12	4.0
3	0.79 (2)	1.52 (3)	341,095	24,194	24	6.6
4	5.28 (5)	17.81 (7)	329,453	72,842	24	18.1
5	3.12 (3)	19.57 (6)	1,346,105	312,022	24	18.8
6	1.01 (2)	2.32 (4)	360,677	299,836	48	45.4

* DPM = disintegrations per minute.

and coral cells were continuously expelled outwards for several minutes (Fig. 4d).

^{14}C-labeling

In the laboratory experiment, translocation of ^{14}C from the labeled to the unlabeled fragment occurred shortly (12–24 h) after fusion (Table I). The percentage of translocated ^{14}C from the total fixed carbon was calculated using the formula: $100 \times U/(L + U)$, where U and L are the total disintegrations per minute (DPM) for the unlabeled and labeled fragments, respectively. The transport of ^{14}C from the labeled to the unlabeled fragment of the colony averaged 2.8% (SD = 1.6; $n = 2$) to 14.5% (SD = 6.9; $n = 3$), 12 to 24 h after fusion, respectively, and increased to 45.4% ($n = 1$) 48 h after fusion (Table I). The coefficient of variability (CV) was high for both the 12-h (CV = 57%) and the 24-h colonies (CV = 47%). The detailed results for tissue samples taken from the unlabeled parts of colonies 5 and 6 (Table I) are provided in Figure 5. ^{14}C-labeled materials extended virtually throughout the unlabeled colonies within 24 to 48 h of fusion, but two neighboring samples differed by 2- to 3-fold, indicating uneven distribution of the ^{14}C-labeled compounds (Fig. 5a, b).

Colonies used in field experiments were much larger than those used in laboratory experiments. Because of the extremely irregular morphology of colonies in nature their actual size could not be estimated; therefore, these colonies were used only in evaluating the translocation distances 24 h after fusion. We recorded ^{14}C in the most distant part of the unlabeled colony, 390 mm away from the fusion line (Fig. 6). However, the amounts of ^{14}C that were recovered within the range of 1–150 mm from the fusion line were significantly higher than the amounts recorded farther away (ANOVA; df = 227; $F = 16.68$; $P < 0.01$). No traces of radioactivity were found in the control colonies for laboratory or field experiments, thus indicating that ^{14}C was not being passed from labeled fragments to the unlabeled parts of the colony through the water.

Discussion

The results presented here show that the gastrovascular system in the soft coral *Parerythropodium fulvum fulvum* is a complex, interconnected network of canals that facilitates the rapid transport of fluid, organic particles, and cells between distant parts of the colony. The movement of the fluid in gastrovascular systems of cnidarians could be driven by contractions of the epitheliomuscular cells (Van Winkle and Blackstone, 1997) or contractile vacuoles (Schierwater *et al.*, 1992), or by the activity of cilia. Since we never observed signs of canal contractions in *P. f. fulvum*, we may conclude that the third possibility, ciliar action, is probably the main mechanism of fluid propulsion in this species, as it is in other anthozoans (Gladfelter, 1983). Furthermore, the gastrovascular system of *P. f. fulvum* may function not only as an internal water system, as previously suggested for other cnidarians

Figure 4. Freely circulating cells in the gastrovascular system of *Parerythropodium fulvum fulvum*. (a) Photomicrograph of the coral cells and zooxanthellae collected from inside the canals of the gastrovascular system. (b) Histological section through the gastrovascular system just below the mouth of a polyp, showing the presence of large numbers of free cells (arrows) inside the gastrovascular system. (c) Closer view of a cross-section of one superficial canal showing the free cells. (d) "Bleeding" of zooxanthellae and coral cells 2 min after injury to the edge of the colony. a = animal cell, b = bleeding, c = canal, ec = ectoderm, en = endoderm, gv = gastrovascular cavity, m = mouth of the polyp, me = mesoglea, z = zooxanthellae. Scale bars: a = 4 μm; b = 200 μm; c = 100 μm; d = 1000 μm.

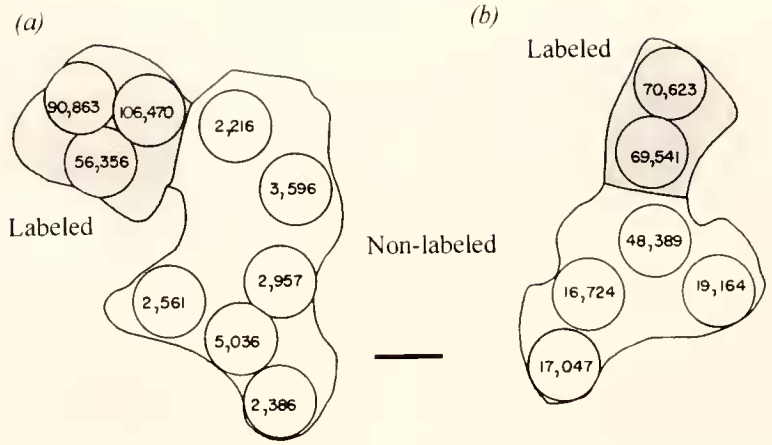

Figure 5. ^{14}C distribution within fused labeled and unlabeled fragments on two laboratory colonies of *Parerythropodium fulvum fulvum:* (a) Colony 5 (Table 1) 24 h after fusion. (b) Colony 6 (Table 1) 48 h after fusion. Circles represent cork-bored samples (0.196 cm^2). Numbers are the disintegrations per minute per sample. Scale bar = 5 mm.

(Chapman, 1974; Fautin and Mariscal, 1991), but also as an effective circulatory apparatus, analogous to a primitive vascular system. The transport of metabolites within *P. f. fulvum* colonies to several tens of centimeters in 24 h is faster than recorded for other corals (Pearse and Muscatine, 1971; Taylor, 1977; Gladfelter, 1983; Rinkevich and Loya, 1983a, b; Rinkevich, 1991) in which transport has been attributed to simple diffusion (Pratt, 1905; Murdoch, 1978a; Fang *et al.*, 1989). This rules out the possibility that the recorded translocation is the result of a process other than gastrovascular transport, as it is in the marine bryozoan *Membranipora membranacea* (Miles *et al.*, 1995).

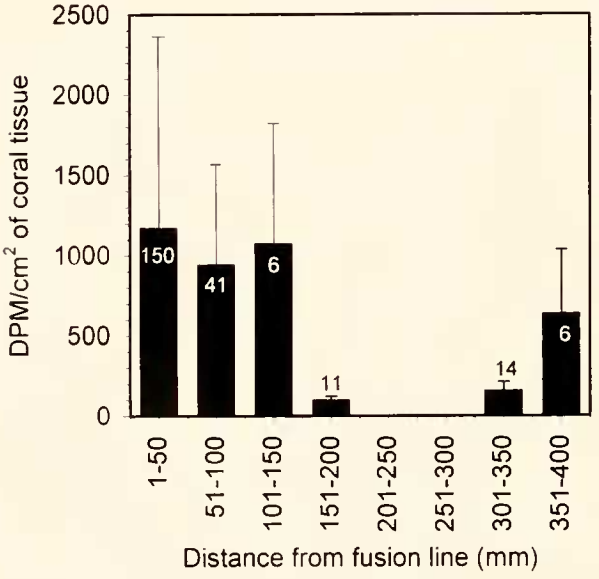

Figure 6. Distribution of ^{14}C within the unlabeled colony of *Parerythropodium fulvum fulvum* in the field experiments (n = 6) 24 h after fusion. Bars indicate the mean number of disintegrations per minute (DPM) per square centimeter of coral tissue (± 1 SD) for the distance range from the fusion line. Numbers at the top of each bar are the sample sizes for each range of distances. No samples were taken between 201 and 300 mm from the fusion line.

The presence of the two distinct networks of canals indicates that they may have different functions. We propose that an important function of the superficial network, which is located just under the upper ectodermal layer and is characterized by narrow canals, slow particle movement, and many dead ends, is to increase the exposure of the algal symbionts to light. The inner network, with larger canals and faster particle movement, is the part of the gastrovascular system responsible for the rapid transport of cells, particles, and substances throughout the colony.

The high variability seen within the 12-h and 24-h measurements of the amounts of ^{14}C translocated from labeled to unlabeled fragments could be due to differences between colonies in the number of functional canal interconnections or the rates of transport. Nevertheless, samples taken from the same colony 24 and 48 h after fusion showed similar levels of fixed ^{14}C, indicating that most of the translocated labeled materials were distributed throughout the unlabeled colony within short periods after fusion. Moreover, the percentage of the total fixed ^{14}C that is translocated is greater if the zooxanthellae that are embedded in the endodermal layer of the labeled fragment, and therefore do not move, are considered. Photosynthates are therefore being transported either inside the circulating algae or as dissolved materials in the gastrovascular fluid.

It is commonly accepted that zooxanthellae are located only in the endodermal layer (Glider *et al.*, 1980; Rinkevich and Loya, 1983a, b; Muscatine, 1990; Gates *et al.*, 1992), whereas free algal cells circulating in the gastro-

vascular system are assumed to be partly digested senescent zooxanthellae or algae in the process of being expelled outside the colony (Trench, 1987; Titlyanov *et al.*, 1996). Our observations suggest that large populations of apparently healthy zooxanthellae within coral cells and animal cells move freely in the gastrovascular system of *P. f. fulvum;* a similar phenomenon is occasionally seen in the hermatypic coral *Acropora cervicornis* (Gladfelter, 1983). Many questions regarding the floating cells remain to be investigated—for example, the digestive behavior of the *P. f. fulvum* gastrovascular system, how healthy living cells are kept from being digested, how long a specific animal cell (with or without symbiontic algae) continues to circulate, and what is the origin of these cells.

Algal circulation probably facilitates metabolite exchange between symbionts and enhances light capture since it acts as a regulatory mechanism for algae. Active intracolonial transport is an important feature of colonial organisms: it allows the reallocation of resources such as oxygen (unpubl. data) and photosynthates, helping to maintain the health of the colony in case of injury or when not all polyps succeed in capturing food or light (Taylor, 1977; Hughes, 1989).

We also have evidence to support the idea (*e.g.*, Buss and Vaisnys, 1993) that the gastrovascular system plays an important role in the bleaching of coral. Previous studies have shown that bleaching may be controlled by extremes of temperature, salinity, and light intensity (Buddemeier and Fautin, 1993). We found that after 1 h of exposure to high temperature (30°C), polyps of *P. f. fulvum* expelled large quantities of zooxanthellae through the mouth (unpubl. data). The mechanisms involved in the regulation of the free-circulating zooxanthellae and animal cells through the mouth of the polyp are not yet understood.

The gastrovascular system in the alcyonarian coral *Parerythropodium fulvum fulvum,* and probably in other cnidarians, plays an important role in the physiology and the development of the colonies, and it may still have other unknown functions, such as that of freely circulating cells.

Acknowledgments

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